Temporal changes in size-at-age: Impacts and implications for reproductive biology, egg density and management of Pacific herring in British Columbia

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ABSTRACT

Age-specific declines in length and weight of Pacific herring occurred in all coastal areas of British Columbia (BC) from approximately 1985 to 2010, followed by a more recent reversal in that trend. Concurrent with declining age-specific size, the number of egg layers deposited on vegetation, as estimated from diver surveys, declined but recently this trend also has reversed. In most areas egg layers declined by half, or more, of pre-decline estimates, from means of about 2–3 layers to about 0.5–1 layers. In general, as egg density declined, no corresponding reductions occurred in other metrics of herring spawning such as the mean length or width of the spawning bed. Correlation analyses indicate that the coherence of these two independently measured trends (declining size-at-age and declining egg density) is highly significant ($p \ll 0.01$) in all REGIONs of the BC coast. We briefly examine two of several potential biological explanations for these temporal changes: (1) size-dependent ovary size; (2) size-dependent packing density of spawning fish. Quantitative estimates of herring spawn deposition are integral to herring spawning stock biomass assessments in BC and elsewhere so it is important to understand the factors that affect egg density. Our analyses indicate that changes in herring growth or 'size-at-age', which probably reflect regional warming related to climate change, can subsequently impact parameters of reproduction and spawning behaviour.

1. Introduction

In the last two decades, there have been developing discussions within the scientific literature about an apparent geographically widespread decline in marine fish growth, often referred to as declining size-at-age. Two general explanations, not mutually exclusive, for such trends are: (1) size-selective fishery removal of larger fish (e.g. Audzijonyte et al., 2013) and (2) climate-change effects leading to increased metabolic costs, and subsequent reduction of energy available for growth (e.g. Baudron et al., 2014). During the last three decades, the size-at-age of Pacific herring (*Clupea pallasi*) has declined over much of its range in the eastern Pacific. During the last 100 years in British Columbia herring have been exploited by intense size-selective fisheries (Hay et al., 1986) but they also have been impacted by gradual changes in temperature and pH of coastal waters (Feely et al., 2008). In British Columbia (BC), herring size-at-age has declined coast-wide in all areas but other biological changes have also occurred including changes in the density of eggs, or egg layers, deposited in coastal spawning locations.

Declines in size-at-age have been described for a number of species,

including herring, in the North Pacific and elsewhere (e.g. Baudron et al., 2014). There are conflicting explanations for such change. Some authors, such as Baudron et al. (2014), invoke warming ocean temperatures caused by climate change as the main cause and suggest that the mechanism can be attributed to climate-induced changes in the trophic conditions or size-dependent, incremental metabolic costs at warmer temperatures. Other studies, while not necessarily dismissing climate change impacts, suggest that selective removal of larger individuals by fisheries may account for some or all of the explanation for a diminution of age-specific size (for example see Fenberg and Roy, 2008 or Neuheimer and Taggart, 2010 and references therein). In BC, some local observers, mainly residents of coastal areas and fishers, suggest that change in egg density (i.e. egg layers) is associated with their perspectives of declining spawning stock biomass (SSB) in recent years/decades.

This paper examines the biological basis for the apparent coherence between two temporal trends in biological data related to Pacific herring off BC: (1) a temporal decline in size-at-age that has been documented for several decades, and (2) a temporal reduction in the number of egg layers based on annual SCUBA diver surveys of herring spawning

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conducted throughout the BC coast. The decline in size-at-age has been described separately in several recent technical stock assessment reports (Cleary and Schweigert, 2011; Cleary et al., 2017). The temporal decline in egg layers was examined in detail by Hay et al. (2011) but no previous attempt has considered the possibility of a functional connection between these trends. The main objective of this paper is to examine evidence for a functional relationship between the annual size composition of spawning herring and the corresponding egg layers deposited in spawning sites. Part of the rationale for such coherence is that fecundity is positively related to size (length) composition (e.g. Hay, 1985) so it is plausible that changes in size composition could lead to corresponding changes in total egg production. It is not obvious, however, that such changes would be accompanied by changes in the density of deposited eggs, as reflected in the estimation of egg layers. To our knowledge such a relationship between fish-size and egg-density has not been examined previously, in herring or other species.

This paper concludes that, contrary to a previous suggestion (i.e. Hay et al., 2011), recent changes in egg layers are not a consequence of changes in survey methodology. Rather the changes in egg layers appear to be a reflection of inter-annual changes in herring growth, probably related to changes in ocean climate.

2. Methods

2.1. Surveys of herring spawn for biomass assessment

Censusing the annual deposition of eggs provides the only fisheries-independent index of abundance used for fisheries assessment and habitat management of Pacific herring throughout the NE Pacific. Annual biomass assessments also rely on age-composition data and annual measurements of age-specific size, as input to age-structured assessment models. In general, the index of egg deposition or spawn index has the largest direct impact on the biomass estimates: when the spawn index is high, the estimated spawning stock biomass (SSB) is high, and vice versa.

Data on the deposition of herring eggs or 'spawn data' have been collected annually, in the main spawning REGIONs of the BC coast since the 1920's (Hay and Kronlund, 1987). For management purposes, the BC coast is divided into geographical areas called REGIONs (Fig. 1). Spawning occurs throughout the coast but tends to be concentrated in certain areas (Fig. 1, bottom panels). Spawn assessment methods have evolved gradually over time. There are two types of spawn surveys: (1) original SURFACE surveys, are conducted on shore or from small vessels. Visual assessments were used to estimate egg density using a simple classification scale that did not allow for estimation of quantitative egg density – or the number of eggs per unit area; (2) more recent DIVE surveys began in the 1980s. SCUBA divers identify macrophytes and other substrates and count <u>egg layers</u> within multiple sampling quadrats spaced along transects that extend from the deepest (subtidal) edge to the highest (intertidal) edge of each herring spawning site. Quantitative estimates of egg density (numbers of eggs/m^2) can be determined with empirical algorithms that relate vegetation-specific egg layer counts to estimates of total egg number per square meter. The detailed methodology of spawn surveys is described in several reports summarized below (Schweigert and Fournier, 1982; Schweigert et al., 1985, 1990; Schweigert and Stocker, 1988; Schweigert, 1993; Hay et al., 2009). The analyses presented in this paper are concerned exclusively with DIVE surveys that focus on the estimate of egg layers and subsequently egg density.

Pacific herring spawning is conspicuous and easy to locate: milt turns shoreline water milky white. Herring spawning usually occurs in episodes of activity, where one episode, hereafter called a spawn 'event' (sometimes called a spawn record in the assessment literature), is separated spatially and temporally from others. Two measures of individual spawn events are the total length along a shoreline and the width (from the deepest sub-tidal depth of occurrence) to the

shallowest (intertidal) area. Some spawn events can be many km long, so there usually are multiple measurements of width. Width assessments, estimated at different parts of the spawn, are used to estimate the total area (in m^2) of each spawn event.

The third key assessment of each spawn event is an estimate of mean egg density (or eggs/m^2). This is done by SCUBA divers who make visual estimates of egg layers. DIVE surveys on a single spawn event consist of multiple estimates of egg layers. Each REGION consists of smaller geographical units called Statistical Areas which can be further divided into SECTIONs (Fig. 2). For each spawn event, transects are located at fixed locations along the coast perpendicular to shore across the width of the underlying algal substrates. Divers begin surveys at the deeper outer margin of the egg bed following the transect line shoreward until eggs are encountered. Sampling frames are placed systematically at 2–20 m intervals depending on the width of the egg bed until the inner edge of the egg bed is encountered and estimates of egg layers on each of six predominant algal groups are noted together with an estimate of the proportion of the sampling frame covered by each algal group. For each sampling frame, the estimate of egg layers and the percent of the sampling frame covered by each algal group are converted to an egg density estimate using a predictive model developed by Schweigert and Fournier (1982). An average egg density weighted by algal group percentage is then calculated for each sampling frame. The mean egg density for the entire spawn event or egg bed is determined assuming a two-stage sampling design (Schweigert et al., 1985). Thus, in contrast to SURFACE surveys, DIVE survey estimates of layers for a single spawn event or egg bed are the mean of many separate measurements, often hundreds. Typically, for a spawn event that consisted of eggs deposited along one km of shoreline, with an average width of 200 m, egg layers would have been evaluated along three different transects (350 m apart), each transect having up to 10 sampling quadrats, resulting in 30 replicate egg density estimates that are then consolidated as a single mean for the spawn event. A total of 4395 records of herring spawn events examined by DIVE surveys were documented within the main assessment areas between 1985 and 2016 (Table 1) with over two hundred thousand estimates of egg layers on vegetation.

2.2. Herring bio-sampling data

Bio-sampling data are collected annually to monitor herring populations in BC. Routine measurements include 'standard' length in mm, total and gonad weight (g) and an evaluation of maturity (with scales of 1–8) using a modified 'Hjort' maturity scale (Hay, 1985). Further, we restricted data to mature, or near-mature females (Hjort stages 4–5) collected in February or March. The sampling data allow estimation of a gonosomatic index (GSI), defined here as the ratio of the gonad weight to the total body weight (sum of the gonad and somatic weight). The collection date, location and fishing gear is also recorded. In general, most samples consist of a random collection of a minimum of 100 fish frozen in a standardized bucket for later examination in a laboratory. We use standard length, defined as the distance (mm) from the tip of the snout to the posterior end of the hyperal plate in the caudal fin. For our analyses length is the preferable measure of size because it was the least impacted by the freezing prior to laboratory measurements. Some fish, especially those frozen at the surface of a container, may lose weight (freeze-dry) and have erroneously low weights.

Gillnets used in Pacific herring fisheries are size-selective, usually taking the largest individuals, so we limited analyses to samples collected by purse seines taken during February and March when fish were close to spawning locations. Most of the fish used in the analysis were at, or close to, prime sexual ripeness.

The average length of herring estimated each year for each REGION or SECTION represents the mean from multiple samples collected from sampling vessels prior to herring fisheries using purse seine nets. In most cases the means represent hundreds to thousands of individual
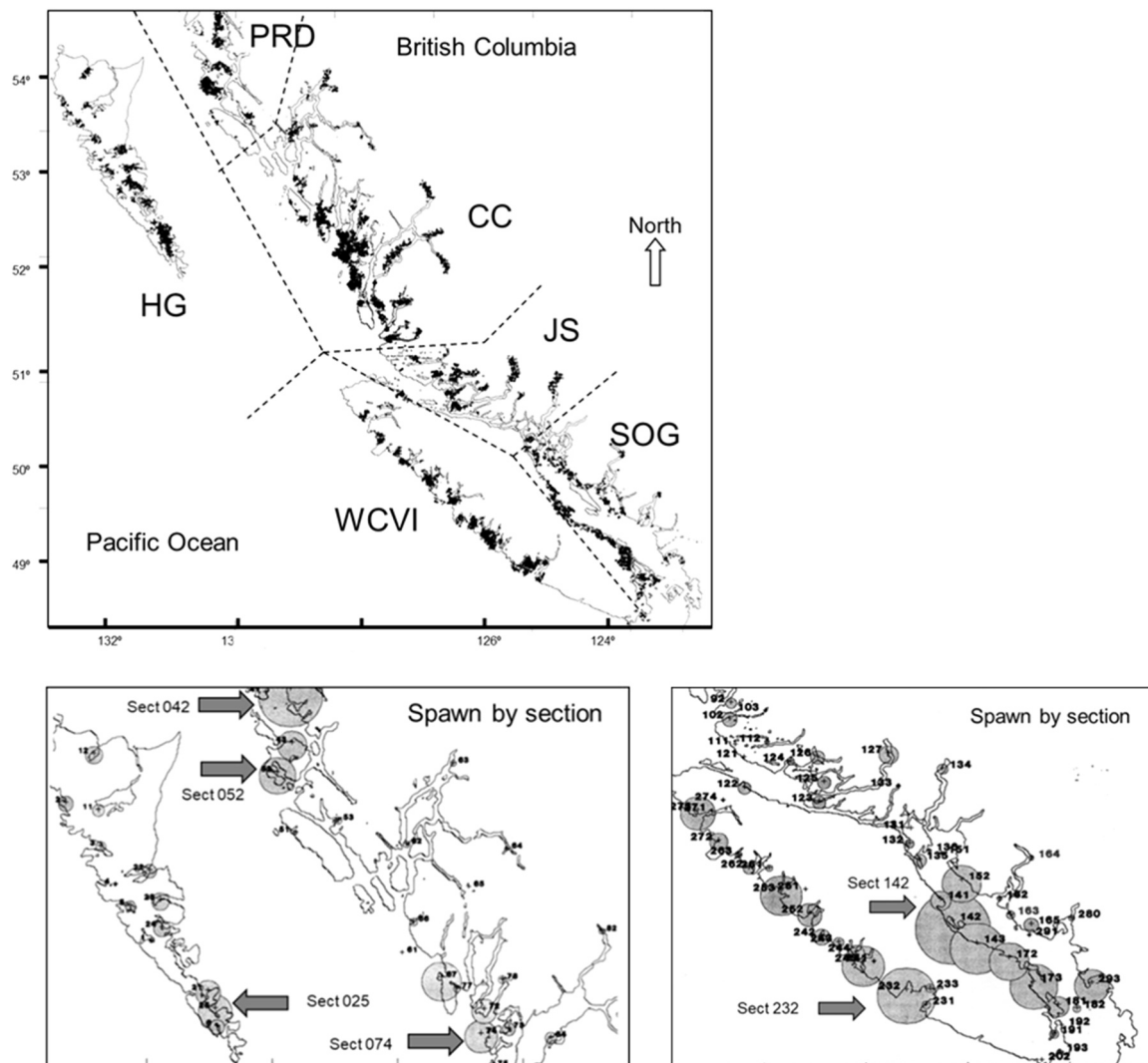
Fig. 1. Spawning areas of the Pacific herring off British Columbia. Top Panel. The coast of British Columbia showing locations of herring spawning locations, as dark stippling, based on nearly 80 years of data. The dashed lines show different REGIONs of the BC coast: (HG refers to the islands of Haida Gwaii; PRD refers to the north coast or Prince Rupert District; CC refers to the Central Coast; JS refers to Johnstone Strait; WCVI refers to the West Coast of Vancouver Island; and SOG refers to the Strait of Georgia. The two bottom panels show relative quantities of herring spawn, indicated by approximate sizes of stippled circles and the arrows indicate the locations of six smaller geographical units called SECTIONs (see Fig. 2) that are selected for detailed analysis and referenced in the text.

herring length measurements.

2.3. Biological basis for covariation between fish size and egg density

We summarized the DIVE survey data both at the REGION level of spatial aggregation and at the SECTION level to evaluate whether the apparent relationship between fish size and egg density occurs both at very broad spatial scale and under more localized conditions. We summarized the bio-sampling data at the same spatial scales.

We also used a subset of bio-sampling data, from (SECTIONs 142–143 - comprising much of Statistical Area 14) in the Strait of Georgia. These SECTIONs were selected for analysis because they support the largest spawning grounds in BC and also because a large number of biological samples were collected there every year with purse seine gear. Analyses examined the relationship between ovary weight and length and GSI and length.

To examine how interannual variation in body size could affect egg density on spawning areas we examined simple models of length-specific packing density in schools (Pitcher and Partridge, 1979) to determine if size-related changes in packing density, combined with length-specific changes in gonad size or egg production, could explain

the observed changes in egg density. We supplemented this analysis by accessing data on length-specific fecundity gathered for several years on BC herring (Hay, 1985).

3. Results

3.1. Temporal trends in egg layers estimated from DIVE surveys

Fig. 3 shows a plot of 52754 estimates of egg layers, estimated by divers, for SECTIONs 142–144 (Statistical Area 14) in the Strait of Georgia. The plot shows that the egg layers vary both within and among years but there was a clear trend for a decrease in layers after about 2005. Fig. 4 shows this trend for a decline in mean egg layers for the larger geographical REGION of the Strait of Georgia and other RE-GIONs. The decline begins in the mid-1990s and ends, in most RE-GIONs, around 2010, when mean layers started to increase (Fig. 4). During the 1985–2010 period egg layers ranged from 1.5 to 2.0 for the three northern/central REGIONs (HG, PRD, and CC) and from 1.5 to 3.0 for the southern REGIONs (WCVI and SOG).
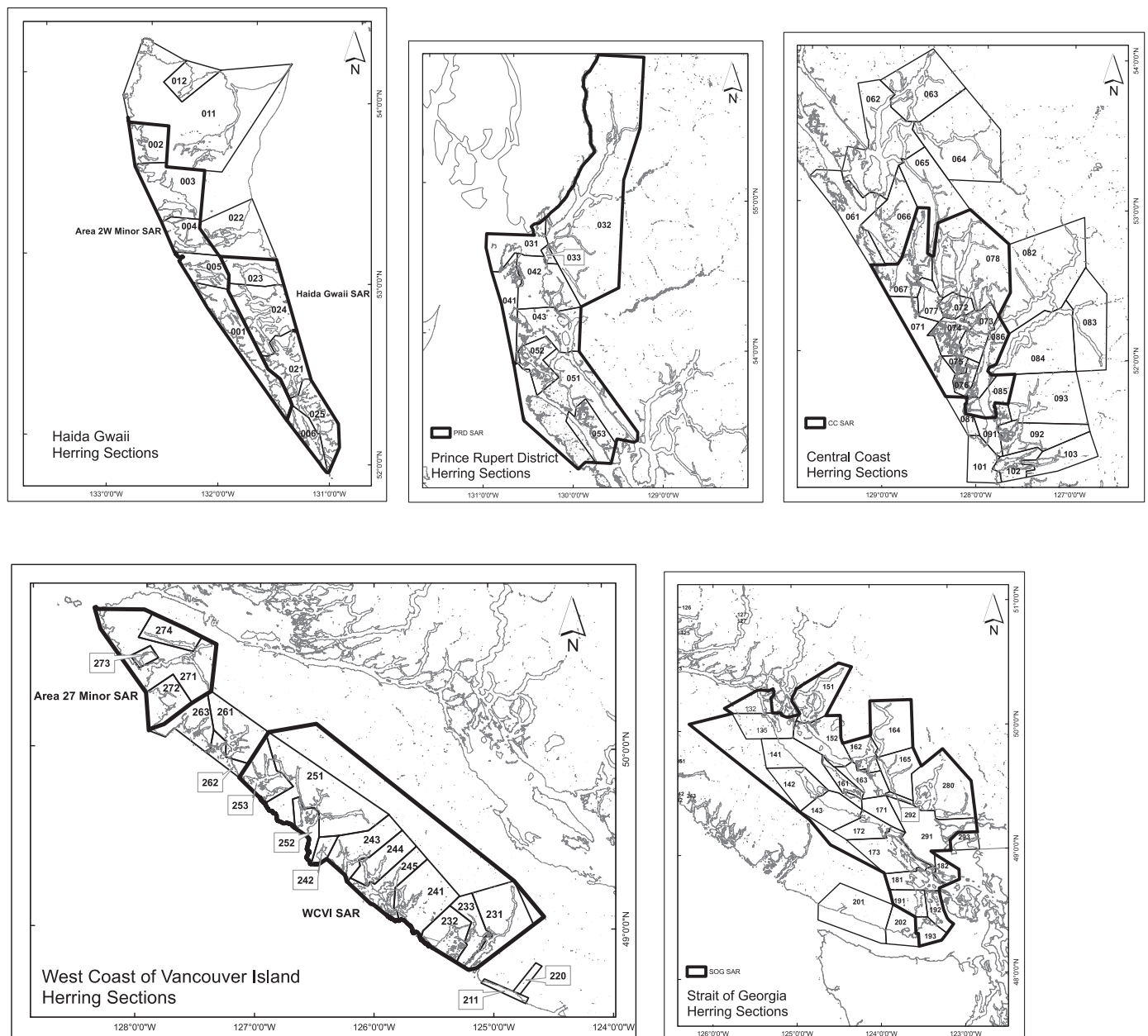
Fig. 2. The coast of British Columbia showing locations of approximately 100 different geographical SECTIONs, differentiated by faint lines. The dark lines show aggregations of SECTIONs within each of the five REGIONs (Fig. 1).

3.2. Temporal variation in size

Fig. 5 shows a decline in mean (standard) length of age-4 herring for each REGION, decreasing from a maximum of 200–210 mm to about 170–180 mm, during 1985 to approximately 2010. The declines are approximately synchronous in all REGIONs and there appears to be a change in the length-at-age trajectories with an increasing trend in mean length starting roughly around 2010. The trajectories and temporal trends, for each REGION, are similar to those noted for the changes in mean egg layers (Fig. 4).

The changes in length-at-age occur in all age groups and have been described elsewhere (Hay et al., 2012; Cleary and Schweigert, 2011) but is illustrated here using mean lengths for only age 4 herring (Fig. 5). Age 4 herring are among the most abundant in the the annual sampling data and fully recruited to the spawning populations (Hay and McCarter, 1999). The temporal trends are very similar in all five RE-GIONs. However, it should be noted that trends in SSB estimates for

each REGION are highly variable (Cleary and Schweigert, 2011). Within the 31-years of data shown in Figs. 4 and 5, the SSB in two REGIONs (HG and WCVI) has generally declined whereas SOG and PRD have generally maintained near average or high SSB levels.

3.3. Temporally coherent trends in fish size and egg layers

Fig. 6 demonstrates positive covariation of mean annual egg layers versus mean length at age 4 for each REGION. Each of the five data sets are significantly correlated with a probability < 0.0001 except for the Central Coast where p < 0.003. The r^2 values are high explaining 28.2, 39.9, 53.3, 69.5% and 60.0% of total variance for REGIONs HG, PRD, CC, SOG and WCVI, respectively. Fig. 6 also shows a fitted regression line which implies that egg layers vary as a function of age 4 fish length. We suggest that a more general functional relationship may exist applying across all age groups, but would require a much more complex and lengthy analysis than we can present here. Specifically, the trend

Table 1
The numbers of DIVE and SURFACE surveys, by year, for each of the five main stock assessment REGIONs of British Columbia.

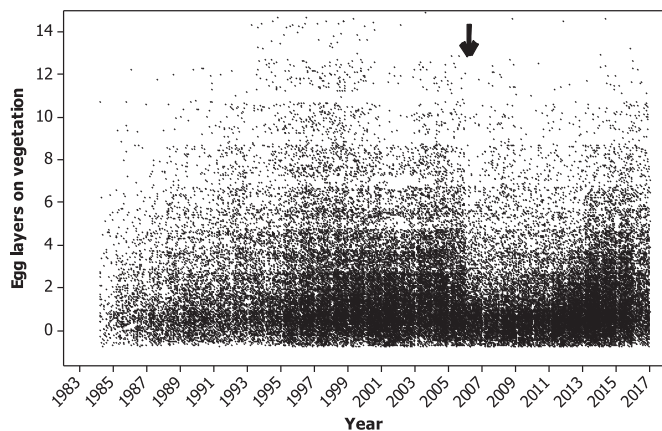| YEAR	HG		PRD		CC		SOG		WCVI	
	SURFACE	DIVE	*SURFACE*	DIVE	*SURFACE*	DIVE	*SURFACE*	DIVE	*SURFACE*	DIVE
1985	*62*	0	*172*	0	*212*	0	*66*	20	*118*	27
1986	*43*	0	*141*	11	*93*	28	*16*	26	*22*	27
1987	*89*	0	*173*	0	*179*	0	*23*	18	*103*	16
1988	*37*	9	*48*	20	*136*	8	*15*	17	*182*	22
1989	*74*	16	*3*	13	*98*	4	*42*	22	*82*	19
1990	*3*	16	*0*	14	*176*	17	*1*	33	*111*	17
1991	*1*	16	*9*	28	*107*	27	*14*	14	*39*	17
1992	*0*	14	*3*	14	*178*	31	*19*	28	*37*	17
1993	*3*	19	*12*	14	*109*	15	*15*	32	*69*	19
1994	*9*	18	*0*	22	*81*	31	*3*	31	*35*	23
1995	*3*	10	*1*	19	*24*	51	*8*	38	*7*	22
1996	*2*	14	*8*	17	*0*	52	*6*	39	*0*	24
1997	*0*	17	*0*	26	*1*	52	*12*	48	*2*	37
1998	*7*	23	*0*	18	*25*	47	*9*	49	*6*	25
1999	*5*	22	*1*	33	*7*	46	*12*	52	*2*	33
2000	*1*	19	*0*	36	*1*	38	*21*	61	*0*	21
2001	*0*	30	*0*	36	*0*	39	*0*	50	*1*	21
2002	*6*	11	*1*	23	*20*	44	*22*	51	*1*	16
2003	*4*	14	*0*	23	*0*	41	*33*	79	*0*	19
2004	*18*	11	*1*	28	*0*	42	*22*	72	*0*	16
2005	*13*	11	*0*	37	*0*	42	*26*	49	*0*	22
2006	*46*	0	*0*	16	*2*	31	*5*	38	*1*	12
2007	*49*	3	*0*	27	*0*	33	*11*	31	*0*	16
2008	*0*	18	*0*	26	*0*	23	*11*	59	*0*	15
2009	*14*	15	*0*	21	*2*	26	*1*	52	*0*	19
2010	*10*	12	*0*	34	*1*	42	*0*	57	*30*	9
2011	*11*	13	*0*	24	*0*	63	*0*	67	*40*	20
2012	*25*	23	*0*	24	*0*	56	*23*	44	*2*	6
2013	*21*	16	*6*	23	*2*	59	*18*	48	*2*	17
2014	*0*	21	*0*	38	*0*	70	*7*	48	*2*	18
2015	*1*	27	*0*	34	*5*	74	*3*	44	*2*	20
2016	*5*	13	*1*	35	*0*	74	*6*	49	*23*	26
All	*562*	451	*580*	734	*1459*	1206	*470*	1366	*919*	638

Fig. 3. Plot of egg layers on vegetation, in SECTIONs 142–144 (Statistical Area 14), as shown in Fig. 2). The data represent 52,754 observations made between 1984 and 2016. Note the decrease in the density of egg layer counts beginning after 2005 (indicated by the downward-pointing arrow). The data shown in this figure contribute to part of the temporal trends, shown as mean annual estimates in Fig. 4, for the SOG REGION.

for decreasing egg layers shown in Fig. 4 was produced by herring of multiple age classes (ages 2–9) whereas Fig. 6 only shows a single age class (age 4). Therefore, a different approach (below) was used to examine the effect of egg density deposited by all age classes.

3.4. The relationship between fish size and egg density (numbers m^{-2})

The results of analyses of time-series data comparing mean fish length and egg density, for 20 individual SECTIONs, are shown in

Table 2, and are similar to the foregoing relationship between fish length and egg layers (Fig. 6). The relationship between mean herring length and egg density, estimated as eggs per square meter, was significant at the 0.001 probability level for two SECTIONs; the 0.01 level for four SECTIONs, the 0.05 level for four SECTIONs and at the 0.1 level (or close) for five SECTIONs. A similar relationship would be expected between fish length and egg layers because egg density estimates are derived from counts of egg layers at individual sampling sites. Fig. 7 shows the relationship between mean herring length and average egg density for six of the 20 key SECTIONs throughout the BC coast. The positive covariation of the fish length:egg density relationship held throughout the coast of BC from very small SECTIONs to the very large spawning SECTIONs (e.g. Section 142 in the Strait of Georgia). Some SECTIONs, such as 025 and 074 are more variable than others probably because in some years there was limited spawning activity and hence relatively few samples available for estimation of egg density. Conversely in some SECTIONs, sometimes there was limited opportunity for collecting biological samples because of the timing of herring movement into the SECTION or reduced availability of fish for determining the mean length accurately.

3.5. Explaining the temporal trends in egg density

Ovary weight (OW) increases exponentially with length (Fig. 8a) and the regression of log (OW) by L is significant (P ≪ 0.01). The mean GSI also increases with length (Fig. 8b). Consequently the reproductive output of a population would increase as a function of fish length. The degree of size-related change in reproductive output is relatively small however, and would not account for the 3- to 4-fold differences in egg layers (Fig. 4) or egg density (Fig. 7) observed over the last three decades.
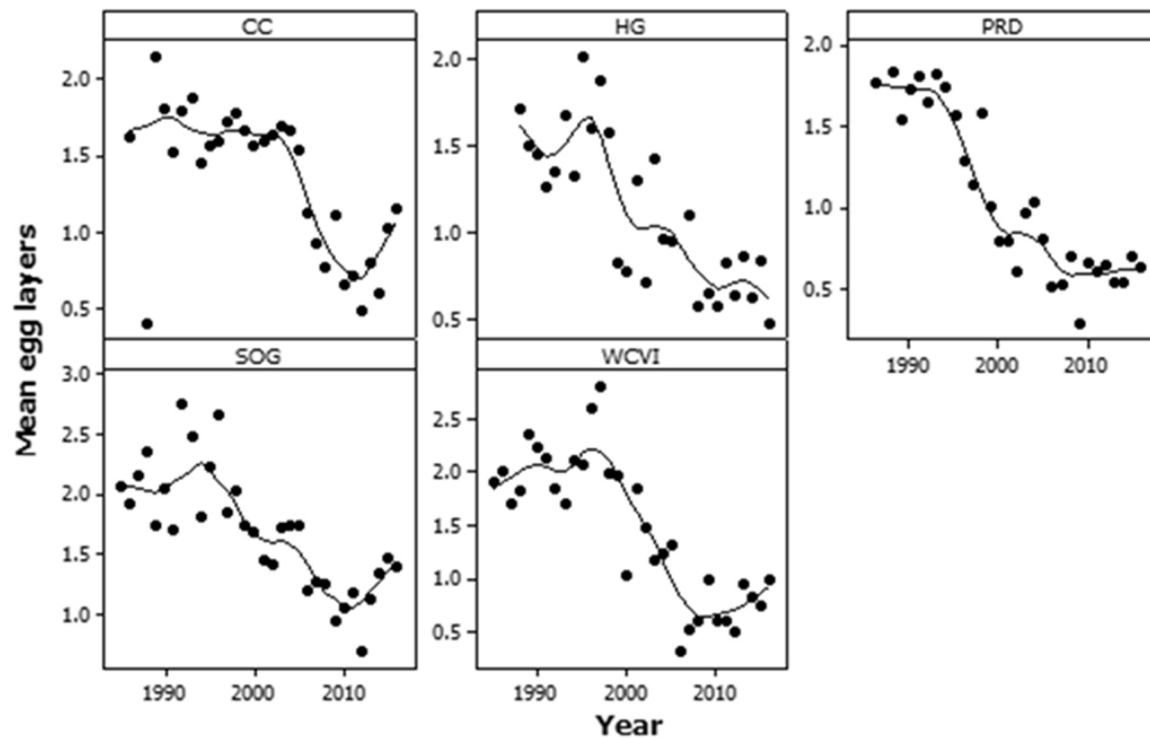
Fig. 4. Temporal change in egg layers from DIVE surveys. Each panel shows the change in mean egg layers, estimated from DIVE surveys and corresponding to each of the five major REGIONs of the BC coast. The solid line represents a Lowess smoother. Note that after a decline, that started in the mid-1990s, the decrease in mean egg layers length stopped in most REGIONs, and started to increase sharply in several.

Herring packing densities, expressed as the numbers of fish per volume, are believed to change as a power function of length (Pitcher and Partridge, 1979; Misund, 1993). Pacific herring spawn mainly in shallow areas and the highest egg densities usually are close to the low

water mark or 'chart datum' (Haegele et al., 1981). When spawning in shallow water fish density would more closely resemble a two-dimensional distribution where packing densities could be limited by the nearest-neighbours laterally in two dimensions, without a vertical third
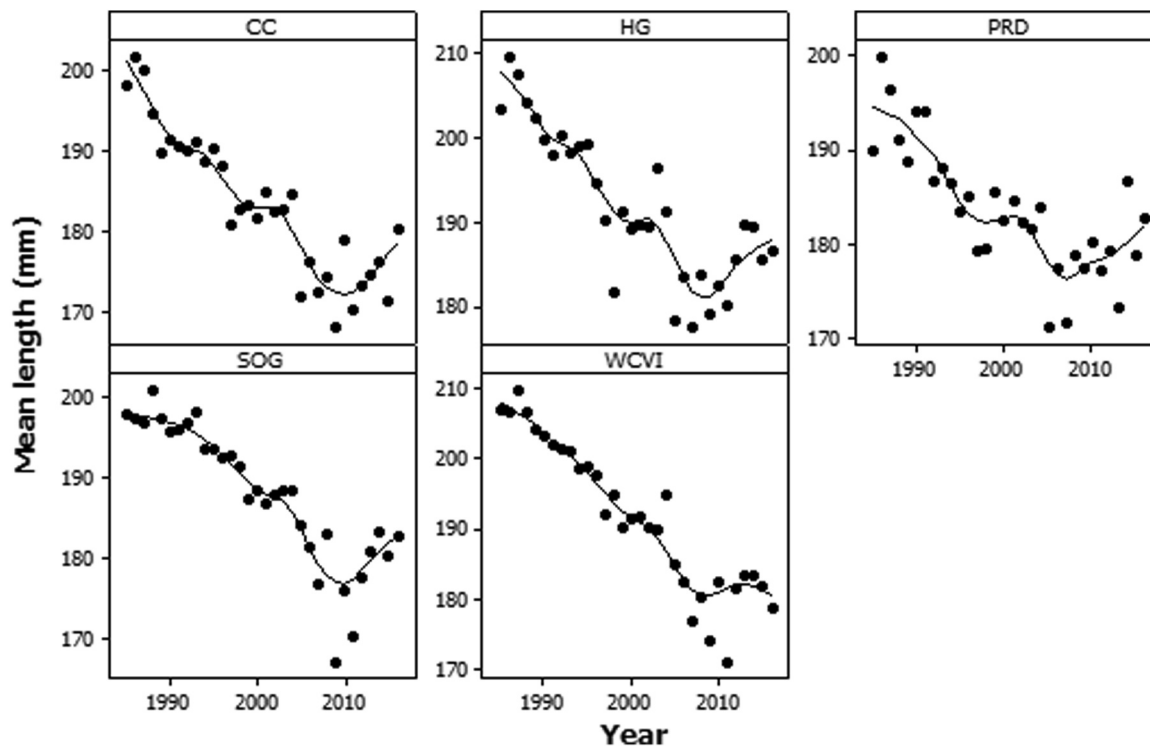

Fig. 5. Change in mean length of age-4 herring. Each panel shows the change in mean standard length (mm) at age 4, corresponding to each of the five major REGIONs of the BC coast. Similar trends occur in all other age groups. The solid line represents a Lowess smoother. Note that after a decline that started in the 1990s, the decrease in length stopped in most REGIONs around the years 2008–2010 and thereafter started to increase sharply.
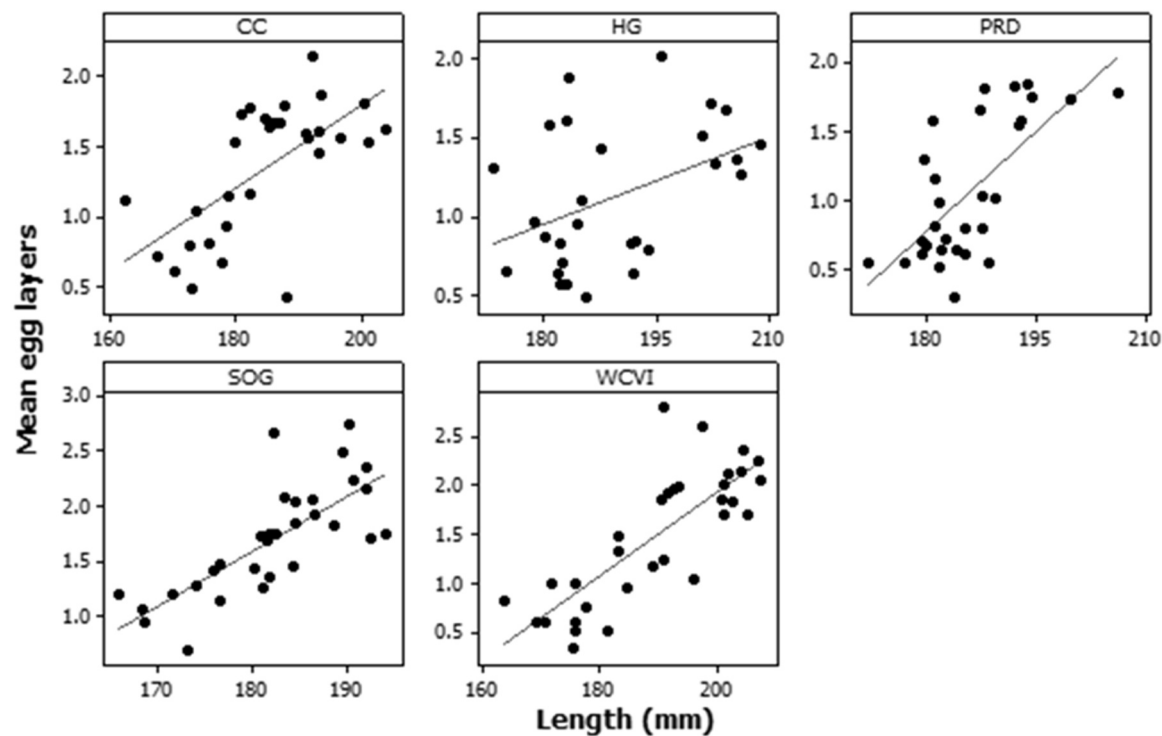
Fig. 6. Egg layers versus fish length. Each panel shows a positive relationship between the mean egg layers and mean length in each of the REGIONs of the BC coast. The length is the mean standard length (mm) of age 4 herring.

Table 2
Summary of regression analyses between the annual mean length (mm) of spawning herring and the annual estimate of mean egg density (eggs m^{-2}) estimated from DIVE surveys, for 20 of the most important SECTIONs on the British Columbia coast. The degrees of freedom (df) indicate the numbers of years used in each regression.

REGION	SECTION	p-value	df	Signif.
HG	006	0.1670	1,8	
	021	0.0352	1,26	*
	025	0.1037	1,26	~0.1
NC	033	0.0048	1,17	**
	042	0.0054	1,28	**
	043	0.8637	1,11	
	052	0.0012	1,28	***
CC	067	0.9335	1,27	
	072	0.0706	1,26	0.1
	074	0.0028	1,26	**
	076	0.1156	1,12	~0.1
	078	0.4518	1,19	
	085	0.0315	1,19	*
SOG	142	0.0220	1,31	*
	143	0.5671	1,28	
	172	0.0796	1,21	0.1
	173	0.0896	1,30	0.1
WCVI	232	0.0001	1,29	***
	243	0.0365	1,18	*
	253	0.0090	1,23	**

Single, double and triple asterisks represent probabilities levels of 0.05, 0.01, and 0.001 respectively.

dimension. Letting the volume (V) in the Pitcher and Partridge equation (V = 0.7 L^3) be equal to the volume of a sphere (V = 4/3πr^3), so 0.7 L^3 = 4/3πr^3, then solving for r provides the length-specific radius of a circle, with area π r^2. This roughly represents the *surface area* (of the bottom) occupied by a single fish of length L and where r is about 0.55L. Table 3 shows the corresponding estimate of egg density (eggs/m^2) that would be expected from a single female at each length if the

eggs were deposited within an area corresponding to the surface area occupied by that female. The analysis indicates that temporal changes in size, leading to changes in packing density, could account for some, but not all, of the observed change in egg density with time (i.e. eggs m^{-2}, as shown in Fig. 7)

4. Discussion

4.1. Changes in size-at-age of herring and other species

Temporal variation in size-at-age is not unique to BC herring. Length-at-age has decreased in all areas of the BC coast, California (San Francisco Bay) and parts of SE Alaska (Hay et al., 2011; Cleary and Schweigert, 2011), in the Atlantic (Wheeler et al., 2009) and in the Baltic (Rajasilta et al., 2015). Similar trends have been described for other species such as Pacific hake (*Merluccius productus*) (King and McFarlane, 2006), rockfishes (*Sebastes*) (McGreer and Frid, 2017) and halibut (*Hippoglossus stenolepis*) (IPHC, 2014) on the Pacific coast and elsewhere. To date, however, the implications of such change on spawning characteristics of herring populations have not been examined.

4.1.1. Can temporal declines in length-at-age explain the changes in egg layers?

It is established that the relative size of gonads, or the GSI (proportion of total body weight consisting of gonads), increases with fish size (Hay, 1985). Fish length and weight are closely related (cubic power function) so it follows that if total length (or weight) changes, then so must gonad size. Fig. 8a shows the relationship between fish length and gonad weight. The increase in gonad weight is not linear and the GSI increases with fish length from about 10–15 in a 140–150 mm fish to more than 25 in fish > 220 mm. Fig. 8b). A consequence is that larger fish would have disproportionally larger ovaries with relatively more eggs than smaller fish, which is consistent with the observation that egg density would change as a function of fish length. However, there has been a recent trend for a slight increase in the length-specific
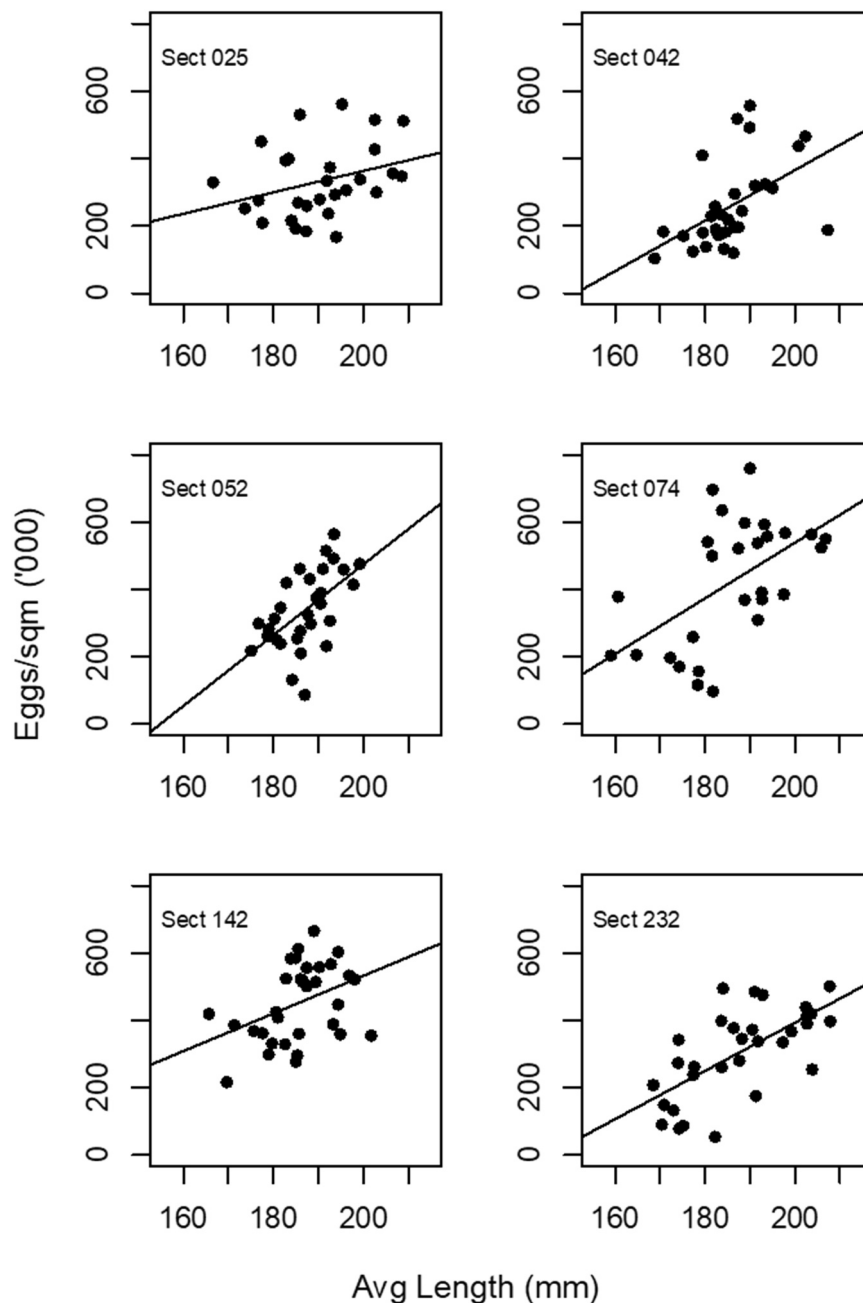
Fig. 7. Relationship between mean egg density (eggs m^{-2}) and mean herring length for six key spawning SECTIONs throughout the BC coast (see arrows in Fig. 1 for locations). The solid line represents a fitted regression which is significant (p < 0.05) for all SECTIONs except HG (Sect 025) where p ∼ 0.1 (See Table 2).

GSI of females in parts of the Pacific (Hay et al., 2012) and similar trends have been documented for Baltic herring (Rajasilta et al., 2015). The explanation for this is not clear but the impact would be to slightly diminish the effect of the apparent fish-length:egg-density trends described in this paper. Therefore although there could be some effect of a change in egg density with a trend for a decrease in length-at-age, the effect would be slight and certainly not sufficient to account for a 3–4 fold change in mean egg layers that has occurred throughout all parts of the BC coast, and perhaps elsewhere. In short, it seems probable that some additional factors might be operational.

4.2. Length-specific packing density: a factor affecting density of spawning herring?

It is established that packing density in herring schools is size-related (Pitcher and Partridge, 1979; Misund, 1993). Therefore, could such a potential change in size-related packing density explain the observed trends in eggs layers? In experimental laboratory studies, Pitcher and Partridge (1979) suggested that the packing density (N/m^3) of herring schools was related to the cube of the length as N = BL^3 where N is the number per unit volume and BL is the body length. Misund (1993) used an acoustical apparatus to develop empirical density estimates for schools of Norwegian Spring spawning herring as N = 2.44BL^3.

BC herring behaviour may not be identical to Norwegian herring and the packing density of herring during spawning may differ from densities at other times of the year. On the other hand, the approximate generality of the cubic relationship between fish number and packing density seems to hold for a number of schooling species (Misund, 1993). Also, it is reasonable to assume that the density (by number) of smaller
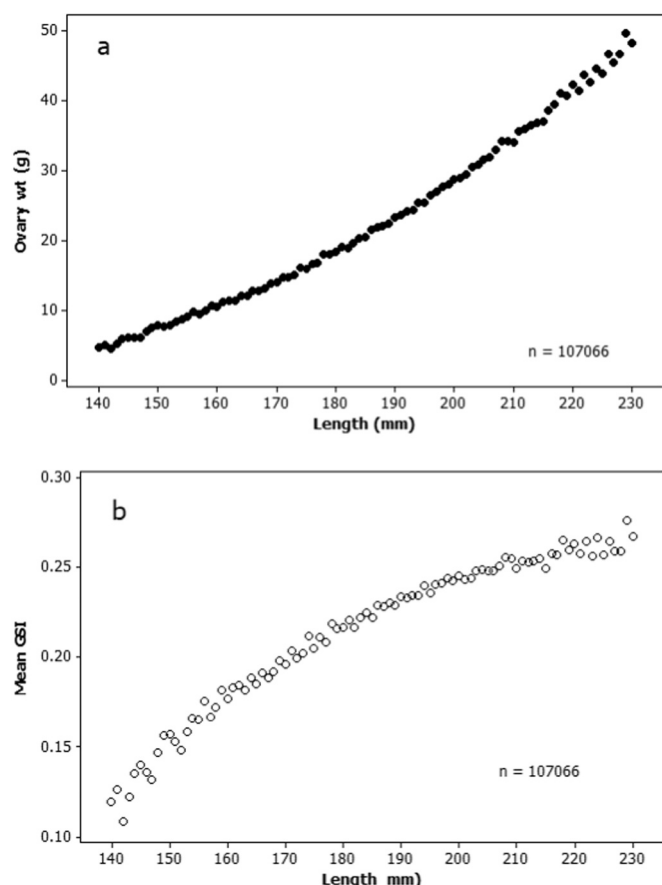
Fig. 8. Length-specific ovary weight and GSI estimate from 107,066 female herring from the Strait of Georgia (SOG) REGION from 1980 to 2016. All fish were captured by purse seines. (a) Top panel: mean gonad weight for each mm length category. (b) Lower Panel: mean GSI (gonosomatic index) for each mm length unit.

Table 3
Estimation of the 2-dimentional area occupied by a single female herring varying in length from 15–28 cm (standard length) and the estimated egg density (eggs/cm^2) if the fish deposited all of its eggs within that area. The fecundity data are empirical estimates based on analyses of Pacific herring collected for three different years from all areas of the British Columbia coast. The numbers are only intended to show that egg density (eggs/cm^2) would increase substantially with length.

L - Fish length-cm	Volume of sphere occupied by 1 fish (0.7 x L^3)	Radius (r) of the spherical volume occupied by fish of length L	Surface area (cm^2) of the circle occupied by one fish - estimated as πr^2	Mean length-specific fecundity (from Hay 1985 and unpublished data)	Estimated eggs/cm^2 deposited by one female
15	2362.5	8.26	214.46	11983	**55.9**
16	2867.2	8.81	244.01	12061	**49.4**
17	3439.1	9.36	275.46	14170	**51.4**
18	4082.4	9.91	308.82	16047	**52.0**
19	4801.3	10.47	344.09	18255	**53.1**
20	5600.0	11.02	381.26	21898	**57.4**
21	6482.7	11.57	420.34	26025	**61.9**
22	7453.6	12.12	461.33	30242	**65.6**
23	8516.9	12.67	504.22	33121	**65.7**
24	9676.8	13.22	549.02	36161	**65.9**
25	10937.5	13.77	595.72	40741	**68.4**
26	12303.2	14.32	644.33	42693	**66.3**
27	13778.1	14.87	694.85	49952	**71.9**
28	15366.4	15.42	747.27	58020	**77.6**

fish might be higher than that of larger fish (i.e. more smaller fish would fit into the same volume as a smaller number of larger fish), even during spawning periods. This was examined by using the Misund (1993) equation to estimate theoretical volumes (m^3) per fish and estimate of numbers of fish per m^3 for each length class. These estimates are theoretical, although they resemble data shown by Misund (1993). The resulting egg density values (Table 3) are not necessarily realistic, but rather the key observation is how the length-specific estimates scale: packing density is lower in smaller herring (16 cm) than larger herring (> 22 cm) and this generality may apply to BC herring. If so, this could add to the potential for a reduction in egg layers as a function of fish size.

4.3. Other factors that might affect egg density: pheromones in the milt

It is established that there are substances in milt that can operate as pheromones to initiate spawning activity both in males and females (Sherwood et al., 1991; Carolsfeld et al., 1997a, 1997b). This experimental evidence indicates that there are lower limits to milt concentration required to initiate spawning. It is conceivable that milt density, when released from a school, could also vary as a function of fish size because larger males, like females, have relatively larger gonads (i.e. higher GSI's) than small males. Therefore the concentrations of gametes, and related pheromone substances might vary with fish size, which, in turn, might affect the initiation and suspension of spawning, and thereby affect egg density.

4.4. Implications for management and conservation

Variation in size-at-age, within and among marine fish species, has attracted attention in recent years. The explanations for such change are still debated and the role of size-selective fisheries, as a causative factor, is mentioned frequently. Size-selective fisheries do occur for Pacific herring but we suggest that other factors, especially energetic factors related to climate change may be important. There are two main arguments to support this: (1) within BC waters, decreases in size-at-age have occurred synchronously in all coastal areas - some with, and others without fisheries (Hay et al., 2012); (2) if size-selective fisheries were the major factor causing changes in size-at-age we would not expect to see the recent reversals of the temporal trends in size-at-age since about 2010 as shown in Fig. 5, because reversals have occurred in areas with fisheries.

An unexpected outcome of our analysis, and perhaps the more useful finding from the perspective of stock assessment and management, is that the inter-dependence of fish length and egg layers provides an independent means of testing for long-term changes in survey methodology. Hay et al. (2011) noted what appeared to be a long-term reduction in egg layers from herring DIVE surveys and investigated the potential for inadvertent or unintentional changes in survey methodology as the probable explanation. Others have challenged the concept and validity of the methodology of the DIVE surveys as the source of a fisheries-independent index and recommend abandoning spawn surveys in favour of other approaches. Our analyses indicate that such a change is not warranted because there appears to be a biological explanation for changes in egg layers as opposed to methodological error. Rago (2005) also warns about impacts of changing survey methods on the accuracy of fishery-independent abundance indices. Potential methodological changes in DIVE assessment of egg layers of Pacific herring could blur any relationships between fish size and egg density. The observation that a single statistically significant relationship exists at both a global and local scale argues for maintaining consistency in the data collection methodology. Monitoring the relationship between fish size and egg density would provide an ongoing indicator of the stability of the survey methodology into the future.

5. Conclusions

The most far-reaching suggestion in this paper is that climate change, or other anthropogenic factors that result in metabolic or trophic shifts leading to a reduction in size-at-age of herring, can affect spawning biology leading to changes in the density of eggs. This, in turn, can affect annual biomass assessments based on spawn surveys and perhaps many other biological factors such as early life history. A specific conclusion is that the DIVE survey estimates of herring spawn, in addition to proving an indispensable fisheries-independent index for assessment of BC herring, also provide an additional perspective of how changes in growth can manifest into changes in other aspects of life history.

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